BIRD SPECIES RICHNESS IN RELATION TO ISOLATION OF ASPEN HABITATS

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ABSTRACT.—We studied 14 stands of aspen (*Populus tremuloides* Michx.) and their associated bird and plant communities in Rocky Mountain National Park, Colorado, in June 1993, to investigate the effects of habitat isolation on bird species richness. Selected aspen stands varied in their degree of isolation from other aspens, but were similar in area, elevation, and vegetation structure. The degree of isolation of aspen stands was expressed in four ways (1) distance to nearest neighboring aspen stand, (2) area-weighted distance to nearest neighboring aspen stand, (3) area-weighted distances of all aspen stands within 1500 m, and (4) total area of aspen stands within 1500 m. Isolation had no significant effect on the bird species richness of the 14 aspen stands studied. Regressions that incorporated isolation and vegetation parameters selected one-variable models, with percent shrub cover (0.5–2.0 m height) accounting for 58% of the variation in bird species richness ($r = 0.76$). Abundant understory vegetation in aspen stands may provide additional cover, food, and breeding habitat to support a larger number of bird species. *Received 8 Mar. 1994, accepted 1 Feb. 1995.*

Aspen (*Populus tremuloides* Michx.) is the most widely distributed native North American tree (Little 1971). Its values include commercial timber production, aesthetics, and wildlife habitat (Crouch 1981). Within the Rocky Mountain region, aspen usually reproduces asexually through suckering following destruction of existing trees (Mueggler 1988). During the last century, there has been little regeneration of aspen, probably because fires have been prevented and suppressed (Crouch 1981). Without regeneration, most aspen stands eventually are invaded and replaced by conifers (Mueggler 1988). Exceptions may be high elevation aspen stands found in mesic sites between moist meadows and Douglas fir (*Pseudotsuga menziesii*) (Marr 1961). The succession of aspen to conifers, along with decreased regeneration of aspen, could lead to future landscapes composed of isolated stands of aspen within large tracts of coniferous forest.

Use of aspen communities by birds for breeding and feeding habitat is well documented (Flack 1976, Winternitz 1980, DeByle 1985, Yahner 1991). Several studies have shown that aspen forests generally support greater bird species richness and total abundance of birds than do other North American montane habitats (Salt 1957, Winternitz 1976, Reynolds

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and Finch 1988). DeByle (1985) listed 134 bird species that use aspen habitats, and aspen may be required habitat for species such as the Red-naped Sapsucker (*Sphyrapicus nuchalis*), Warbling Vireo (*Vireo gilvus*) and MacGillivray's Warbler (*Oporornis tolmiei*) (Reynolds and Finch 1988).

Bird species richness in aspen communities probably varies with the degree of isolation of stands as predicted by MacArthur and Wilson's theory of island biogeography (MacArthur and Wilson 1967). Based on that theory, one would expect lower species richness in more isolated habitats. Although the use of aspen for timber products is increasing, the main reason for harvesting aspen in Colorado is to increase regional vegetation diversity by stimulating aspen growth (D. Lowry, USDA For. Serv., pers. comm.). Most aspen stands that are harvested are four hectares or less. This size represents the majority of stands found along the front range, although larger stands can be found in southwestern Colorado. Current management of aspen in the Arapaho and Roosevelt forests of Colorado, involving the cutting of small stands (<4 ha) (D. Lowry, USDA For. Serv., pers. comm.), could lead to landscapes that support only isolated pockets of aspen in a matrix of other vegetation types. The following research was developed to investigate the effects of isolation on bird species richness in aspen stands.

STUDY AREA AND METHODS

Fourteen aspen stands were selected in Rocky Mountain National Park (RMNP) for this study. RMNP is located along the Continental Divide, adjacent to Estes Park, Colorado. Elevations range from 2438 to 4345 m. The landscape is composed mostly of glacier-sculpted valleys, rugged peaks, montane and subalpine forests, and alpine tundra (U.S. National Park Service 1988). This study area was selected because aspen stands within the Park are not currently managed. We assume the stands are undisturbed by humans and have naturally evolved to their current form.

Only 0.5% of the Park's 107,980 ha is dominated by aspen (*Populus tremuloides* Michx.) (R. Thomas, USDI Natl. Park Serv., pers. comm.). The understory in aspen groves consists mainly of common juniper (*Juniperus communis*), barberry (*Mahonia repens*), kinikinnick (*Arctostaphylos uva-ursi*), Wood's rose (*Rosa woodsii*), huckleberry (*Vaccinium* spp.), strawberry (*Fragaria* spp.), heartleaf arnica (*Arnica cordifolia*), golden banner (*Thermopsis divaricarpa*), sedges (*Carex* spp.), fescues (*Festuca* spp.), and geranium (*Geranium* spp.). Aspen habitats in RMNP have been used heavily by elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*) for food and shelter (Stevens 1976). Effects of ungulate grazing on bird community structure within aspen habitats of RMNP are not known. In addition, since 1978, fire suppression has retarded the regeneration of aspen habitats within the Park. However, prescribed fires, with the sole purpose of rejuvenating aspen habitats, are included in the 1994 management plans (J. Conner, pers. comm.).

Aspen stands initially were selected using RMNP data in a geographic information system (GRASS#4.0; USACERL 1991). These data were used to generate maps of aspen stands that were categorized by diameter class (dbh) and percent canopy closure (% cc). We at-

tempted to select stands that varied in their degree of isolation from other aspen stands but were similar in area, elevation, and vegetation structure. Fourteen study stands were selected based on the following criteria: (1) average dbh >10 cm, (2) % cc >60%, (3) at least ¾ of the stand perimeter surrounded by conifers, mainly lodgepole pine (*Pinus contorta*), (4) elevation between 2500 m and 3500 m, (5) stand area 1–2 ha, (6) varying degrees of isolation from other aspen, and (7) within 2 km access from a trail or road. Many of the stands initially selected from these maps were eliminated after ground-truth surveys indicated they did not meet the above criteria. Additional stands were located using aerial photos which proved to be more useful in locating small isolated aspen stands than was the GIS database.

We surveyed each aspen stand three times for birds during June 1993. Data on species identity, number, and distance from observer were recorded for all birds seen or heard at the center of each stand and at a point located at least 100 m outside of each stand in the surrounding conifer forest, using variable circular plots (Reynolds et al. 1980). The conifer surveys were included to confirm that surrounding bird communities were similar around all 14 aspen stands. Surveys began after sunrise and continued until 11:00 h MST. Following a one-min rest period, a 10-min counting period was conducted at each point. Birds flying above the stands were not recorded.

We measured a variety of stand structural characteristics, as described below, to ensure that we selected aspen stands with similar structures. Plant species composition was not estimated because bird distributions and abundances generally are more closely correlated with habitat physiognomy (Anderson and Shugart 1974, Roth 1976, Cody 1981).

Vegetation was sampled at six random points within each aspen stand during June 1993. Random points were chosen by gridding each stand, then randomly picking coordinates within the grid. Sampling employed both line transects and 15-m radius circles. Canopy closure (>5 m), sub-canopy cover (2–5 m), shrub cover (0.5–2 m), and ground cover (<0.5 m) were sampled by noting the presence or absence of vegetation every 3 m along each of three, 15-m transects initiated at each random point. Each transect orientation was based on a reading from a secondhand watch. The reading was converted to degrees by adding a zero. Percent water cover was also recorded because Winternitz (1980) observed a correlation between the presence of standing water and high bird species richness and breeding bird density in aspen habitats of Colorado. Canopy height was estimated by taking a clinometer reading for one aspen tree at each random point. All trees located within a 15-m radius circle surrounding each random point were counted and placed into one of five diameter classes: 0–5 cm, 5–10 cm, 10–20 cm, 20–30 cm, and >30 cm. This information was used to estimate stand basal area, snag basal area, mean diameter, and percent aspen within each stand (Mueller-Dombois and Ellenberg 1974).

Area of each stand was estimated, as were the areas of and distances to all other aspen stands within 1500 m of each study site. Areas and distances were estimated by digitizing 1987 aerial photos in ARC/INFO (Environmental Systems Research Institute 1991).

Basis for 1500 m isolation distance.—Bird surveys were conducted during June, at which time all local bird species were breeding (pers. obs.). We assumed that breeding birds remained in or near their territories at this time. A distance of 1500 m was selected because it exceeds the territorial and home range diameters of most forest bird species (Brewer 1963, Schoener 1968, Kroodsma 1973, Zach and Falls 1979, Mellen et al. 1992).

Calculations for isolation effects.—Isolation effects were assessed using several different measures of isolation: (1) distance to nearest neighboring aspen stand, (2) area-weighted distance to nearest neighboring aspen stand, (3) area-weighted distances of all aspen stands within 1500 m, and (4) total area of aspen stands within 1500 m. Area-weighted distances were calculated using a negative exponential function, where species richness was assumed

TABLE 1

ESTIMATES OF AREA, NEAREST NEIGHBOR DISTANCE, NEAREST NEIGHBOR AREA-WEIGHTED
DISTANCE (WD), AREA-WEIGHTED DISTANCES TO ALL ASPEN WITHIN 1500 M (WD 1500 M),
AND TOTAL AREA OF ASPEN WITHIN 1500 M FOR 14 ASPEN SITES

Site	Area (ha)	Distance (m)	WD	WD 1500 m	Total (ha)
E1	2.6	35	2.69	5.2	34
E2	1.4	63	0.66	3.8	23
E3	0.8	44	0.70	4.6	25
E4	1.4	63	1.48	4.6	21
E5	1.3	344	0.17	1.8	14
W1	1.1	74	1.59	7.4	53
W2	3.9	425	1.08	2.3	50
W3	3.2	493	0.28	2.0	21
W4	5.0	123	0.48	5.6	59
W5	1.0	218	0.41	0.6	3
W6	0.8	218	0.51	0.8	4
W7	1.9	80	1.72	4.9	27
W8	2.2	37	0.71	5.8	26
W9	2.1	13	0.77	6.4	26

to decline exponentially as distance increased. We assumed that 1% of birds present in aspen stands dispersed greater than 1500 m during the breeding season. Using this assumption, the relationship between species richness and isolation distance is: $0.01 = \exp(K \times \text{distance}_{max})$, where: $\text{distance}_{max} = 1500$ m, and K = slope of negative exponential function. Solving this equation for K gives a value of -0.0031. A weighted distance value (V) for each stand was calculated as $V = \exp(KD)$, where: $K = -0.0031$ and D = distance to the nearest neighboring aspen stand (m). An area-weighted distance (WD) was calculated as $WD = VA$, where V = weighted distance value and A = area of the nearest neighboring aspen stand (ha). An area-weighted isolation index incorporating all aspen stands within 1500 m (WD 1500 m) was then calculated by summing the area-weighted distances to all stands within 1500 m.

Table 1 lists the area and estimates of the various isolation measures for each aspen stand. Area-weighted isolation indices with low values represent stands that were isolated and/or had small amounts of surrounding aspen. Conversely, high values represent stands that were not isolated and/or had large amounts of surrounding aspen. The area-weighted isolation index provides an estimate of the effective or "nearby" area of available habitat. This index should be related to the expectation of dispersal for breeding birds within aspen habitat. Aspen stands with high "nearby" area estimates would be expected to maintain greater species richness than stands with low "nearby" areas.

The isolation indices calculated above, along with vegetation parameters, were incorporated into several stepwise multiple regressions (PROC REG; SAS Institute, Inc. 1987) to investigate the effects of isolation on bird species richness in aspen habitats. Vegetation parameters and isolation categories were used as independent variables and bird species richness as the dependent variable. Because several isolation categories correlated with each other, separate stepwise multiple regressions were run using each of the following isolation categories: (1) distance to nearest neighboring aspen stand, (2) area-weighted distance to

TABLE 2

MEANS AND RANGES FOR ALL VEGETATION PARAMETERS SURVEYED IN 14 ASPEN STANDS

Parameters	Mean	Range
Diameter (cm)	15.6	13.2–20.3
Height (m)	12.4	9.8–15.8
Water cover (%)	4.1	0–24.2
Ground cover (%)	59.3	34.5–83.2
Shrub cover (%)	16.3	1.2–31.0
Sub-canopy cover (%)	7.5	0–24.3
Canopy closure (%)	65.5	54.7–81.3
Aspen (%)	82.3	59.2–94.5
Basal area (m^2)	762.4	527.9–1560.3
Snag basal area (m^2)	77.6	29.5–184.2

nearest neighboring aspen stand, (3) area-weighted distances of all aspen stands within 1500 m, and (4) total amount of aspen stands within 1500 m. Stepwise multiple regressions were also done using area-weighted distances of all aspen stands and total amount of aspen stands within 500 m and 1000 m. Vegetation parameters among stands were compared using the Kruskal-Wallis nonparametric test (PROC ANOVA; SAS Institute, Inc. 1987). A separate average species richness estimate was calculated for each aspen stand and the surrounding conifers based upon three bird counts. Differences in bird species richness among aspen stands and conifers were tested by analysis of variance (PROC ANOVA; SAS Institute, Inc. 1987). Frequency distributions of bird species richness for aspen and conifer birds were compared by calculating a Kolmogorov-Smirnov test statistic (PROC NPAR1WAY; SAS Institute 1987).

RESULTS

Aspen stands were located throughout RMNP, with five on the east side of the Park and nine on the west side. All vegetation parameters were significantly different ($P < 0.01$) among the 14 stands (Table 2). Aspen stands satisfied all initial selection criteria except for stand area. Stand areas differed substantially, ranging from 0.8 ha to 5.0 ha (Table 1). Regression analysis of stand area and bird species richness was non-significant ($P = 0.62$); therefore, we assumed that species richness was not affected by differences in stand areas of the 14 aspen stands studied. Elevations for the 14 stands ranged from 2500 m to 3100 m. The distance between a stand and its nearest neighboring aspen stand ranged from 13 m to 493 m (Table 1). The total area of surrounding aspen stands within 1500 m varied between 3 ha and 59 ha (Table 1).

A total of 23 and 15 bird species were observed in aspen and conifer forests, respectively (Table 3). The most abundant species in aspen were Mountain Chickadee (scientific names in Table 3), American Robin, and

TABLE 3

BIRD SPECIES OBSERVED IN BOTH ASPEN AND CONIFER HABITATS, THE NUMBER OF STANDS
EACH SPECIES WAS OBSERVED IN, AND THE TOTAL MINIMUM NUMBER OBSERVED

Species	Aspen		Conifer	
	Stands	Minimum[a] individuals	Stands	Minimum individuals
Broad-tailed Hummingbird (*Selasphorus platycercus*)	9	11	9	12
Northern Flicker (*Colaptes auratus*)	1	1	0	0
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	4	6	0	0
Hairy Woodpecker (*Picoides villosus*)	2	3	0	0
Downy Woodpecker (*P. pubescens*)	0	0	1	1
Olive-sided Flycatcher (*Contopus borealis*)	1	2	0	0
Empidonax spp.	4	4	1	1
Western Wood-Peewee (*Contopus sordidulus*)	3	3	0	0
Tree Swallow (*Tachycineta bicolor*)	2	3	0	0
Gray Jay (*Perisoreus canadensis*)	2	2	3	5
Jay spp.	1	1	0	0
Black-capped Chickadee (*Parus atricapillus*)	2	2	1	1
Mountain Chickadee (*P. gambeli*)	12	26	8	13
Chickadee spp.	3	3	2	3
Red-breasted Nuthatch (*Sitta canadensis*)	1	2	1	1
Brown Creeper (*Certhia americana*)	1	2	1	2
House Wren (*Troglodytes aedon*)	3	5	0	0
Ruby-crowned Kinglet (*Regulus calendula*)	7	8	8	11
American Robin (*Turdus migratorius*)	13	22	8	10
Warbling Vireo (*Vireo gilvus*)	12	20	4	5
Yellow-rumped Warbler (*Dendroica coronata*)	9	10	8	10
Sparrow spp.	2	2	0	0
Dark-eyed Junco (*Junco hyemalis*)	12	15	13	17

TABLE 3
CONTINUED

	Aspen		Conifer	
Species	Stands	Minimum[a] individuals	Stands	Minimum individuals
Brewer's Blackbird (*Euphagus cyanocephalus*)	1	1	0	0
Pine Siskin (*Carduelis pinus*)	4	5	5	7
Red Crossbill (*Loxia curvirostra*)	0	0	1	1
Finch spp.	1	1	0	0
Unidentified	13	24	13	21

[a] Minimum number of individuals was determined to be the greatest number of individuals seen during any one of three counting periods.

Warbling Vireo. The most abundant species in conifer were Mountain Chickadee, Broad-tailed Hummingbird, and Ruby-crowned Kinglet.

The majority of species occurred in only one or two sites (Fig. 1). No species was seen in all 14 aspen or 14 conifer sites. The above distributions were non-significant ($K_{sa} = 0.6$, $\alpha = 0.05$), indicating that the frequency distributions of bird species richness for aspen and conifer birds were similar. Bird species richness differed significantly ($P = 0.003$) among the 14 aspen stands. Differences in bird species richness among conifer sites were also tested and were non-significant ($P = 0.40$, power $[1 - \beta] = 0.49$). Average bird species richness was significantly higher in aspen than in conifer habitats ($P < 0.0005$).

All stepwise multiple regressions selected one-variable models, with percent shrub cover (0.5–2 m height) as the only significant predictor variable. Variation in the density of the shrub understory accounted for 58% of the variance in bird species richness ($R^2 = 0.58$, $r = 0.76$) (Fig. 2). The prediction equation was: $\hat{y} = 5.13 + 0.16$ (shrub cover).

DISCUSSION

Our results show a high degree of variability in vegetation structure among aspen stands in RMNP. Although vegetation parameters varied among stands, certain parameters appear to be more influential than others in determining bird community structure. In this study, the amount of understory vegetation appeared to be the main determinant of bird species richness. The presence of vegetation in the shrub layer may benefit birds by providing cover and increasing food availability. Percent shrub cover (0.5–2.0 m height) was highly correlated with bird species richness ($r =$
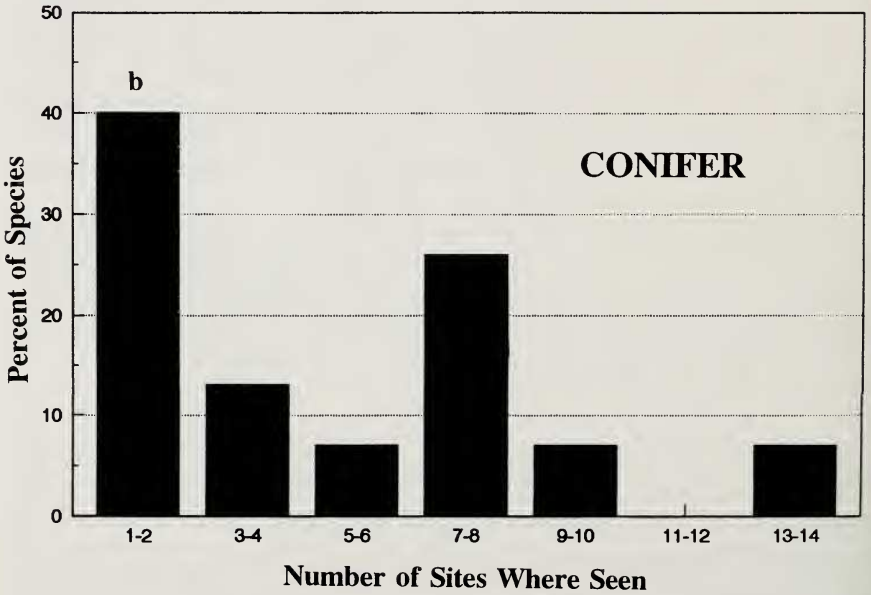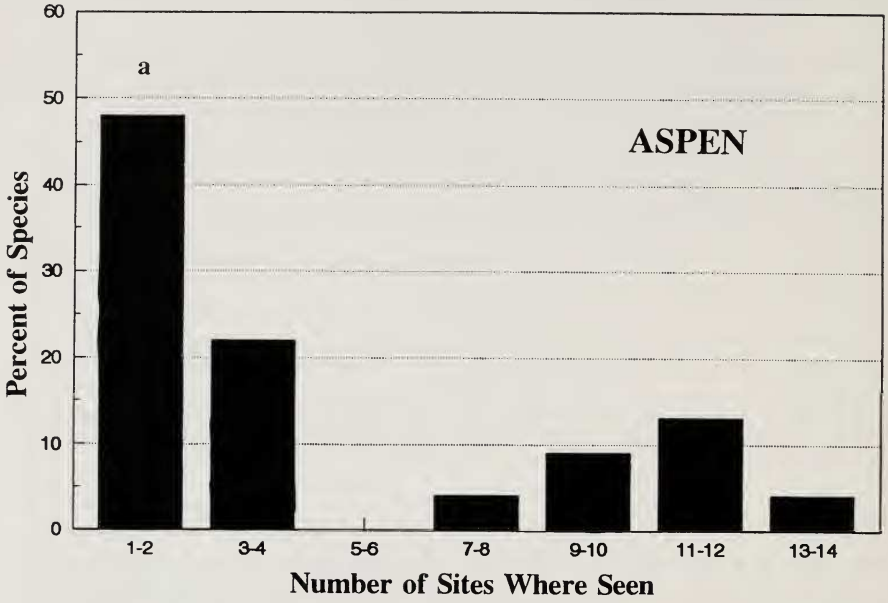
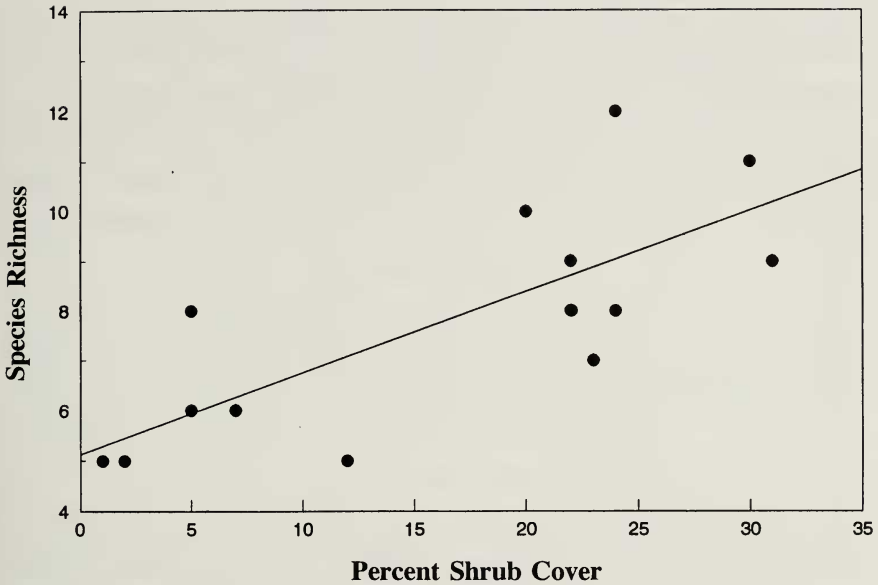FIG. 1.   Percent of all species that were seen in (a) 14 aspen sites and (b) 14 conifer sites in RMNP, Colorado.

FIG. 2.   Regression of shrub cover (0.5–2 m height) and bird species richness ($P = 0.0015$; $R^2 = 0.58$).

0.76, $P = 0.0015$). A recent study by Mills et al. (1991) reported a strong correlation between total vegetation volume and breeding bird density. This suggests that bird density and species richness may reflect the overall abundance of resources. Our results corroborate such suggestions.

On average, aspen sites contained a higher species richness than did surrounding conifer sites. Eight species were observed in aspen that were not observed in conifer: Northern Flicker, Red-naped Sapsucker, Hairy Woodpecker, Olive-sided Flycatcher, Western Wood-Peewee, Tree Swallow, House Wren, and Brewer's Blackbird. Some of these species, such as the Red-naped Sapsucker may require aspen for survival and reproduction (Reynolds and Finch 1988). Therefore, even small stands of aspen, such as those studied, may be important in supporting populations of birds that require aspen for survival and reproduction, thus maintaining the overall species richness in the landscape.

Isolation had no significant effect on bird species richness within the 14 aspen stands studied. Several hypotheses may explain these results: (1) isolation distances greater than the maximum considered here (493 m) may be necessary before isolation effects are observed, (2) other factors which were not studied may overshadow the effects of isolation (e.g., predation rates, competition, food availability, disease), (3) bird species

richness may be more influenced by vegetation structure than by isolation, and/or (4) isolation does not influence bird species richness in aspen communities because this habitat is intrinsically highly fragmented.

Previous studies of isolation effects on bird species richness produced varying results. Johns (1993) observed that the presence of forest interior bird species was influenced by both aspen grove size and isolation. Whitcomb et al. (1981) stated that isolation was an important factor in determining the presence of forest interior bird species in lowland deciduous forests in Maryland. Yet, Lynch and Whigham (1984) showed that the species richness of forest interior birds in Maryland was related only to area and isolation when differences in vegetation were controlled. Martin (1980) concluded that area was more important than isolation or vegetation structure in determining bird abundance and species richness in shelterbelts of South Dakota. A decline in the bird species richness of pine forests in France was shown to coincide with decreasing patch size and increasing isolation (Lescourret and Genard 1994). Lescourret and Genard believed the effect could be attributed to a variation in vegetation structure and altitude. Isolation was shown to affect bird species richness negatively in forest islands in Wisconsin once area effects had been taken into account (Howe 1984).

Our limited evidence suggests that other habitat variables, notably habitat structure, may be more important than habitat isolation in determining bird species richness in aspen communities of Colorado. Furthermore, species-specific isolation effects may not be reflected by changes in overall species richness. Since species respond differently to habitat variations, isolation effects may be more appropriately studied by investigating individual species. This was not attempted in this study because of limited numbers of observations for most species.

Although the results from this study suggest that isolation had little effect on the bird species richness of small aspen stands, the effect of isolation on individual species needs to be investigated. Until species-specific data are obtained, managers should not disregard the possible influence of habitat isolation on bird communities. We recommend that population studies focus on some or all of the eight species we observed only in aspens.

Because bird species richness correlated significantly with shrub cover ($r = 0.76$), we would recommend management techniques that maintain or produce abundant understory vegetation in aspen habitats. Understory development might be enhanced by controlling grazing pressure by elk and mule deer.

This study begins to investigate the effects of landscape patterns on bird species richness. Further studies which employ manipulation of land-

scape patterns and long-term monitoring of trends in bird species occurrence should be supported. Areas with highly isolated aspen habitats and areas with non-isolated habitats should be compared over several decades for differences in species abundances, composition, and richness. The survivorship and fitness of individuals among isolated and non-isolated habitats should also be investigated before the true effects of isolation may be known.

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